ISSN 0704-3716

Canadian Translation of Fisheries and Aquatic Sciences

No. 5328

Contributions to the systematics of the African Naididae (Oligochaeta). III. Studies on the qualitative and quantitative chaetotaxonomy of the Naididae

Reinmar Grimm

Original title: Beitrage zur systematik der afrikanischen Naididae (Oligochaeta). III. Untersuchungen zur qualitativen und quantitativen Chaetotaxonomie der Naididae

In: Mitt. Hamb. Zool. Mus. Inst., 83: 101-115, 1986

Original language: German

Available from:
Canada Institute for Scientific and Technical Information
National Research Council
Ottawa, Ontario, Canada K1A 0S2

1987

28 typescript pages

Secretary of State / Secrétariat d'État

90-02099/

MULTILINGUAL SERVICES DIVISION – DIVISION DES SERVICES MULTILINGUES

TRANSLATION BUREAU BUREAU DES TRADUCTIONS

LIBRARY IDENTIFICATION – FICHE SIGNALÉTIQUE

Translated from - Traduction de	Into - En
German	English

Author - Auteur

Reinmar Grimm

Title in English or French - Titre anglais ou français

Contributions to the Systematics of the African Naididae (Oligochaeta)

III. Studies on the Qualitative and Quantitative Chaetotaxonomy of the Naididae

Title in foreign language (Transliterate foreign characters)
Titre en langue étrangère (Transcrire en caractères romains)

Beiträge zur Systematik der afrikanischen Naididae (Oligochaeta).

III. Untersuchungen zur qualitativen and quantitativen Chaetotaxonomie der Naididae

Reference in foreign language (Name of book or publication) in full, transliterate foreign characters.
Référence en langue étrangère (Nom du livre ou publication), au complet, transcrire en caractères romains.

Mitt. hamb. zool. Mus. Inst.

Reference in English or French - Référence en anglais ou français

Report from the Zoological Museum and Institute of Hamburg

Publisher - Éditeur	DATE OF PUBLICATION / DATE DE PUBLICATION			Page Numbers in original / Numéros des pages dans l'original
	Year / Année	Volume	Issue No. / Numéro	101 - 115
Place of Publication / Lieu de publication				Number of typed pages / Nombre de pages dactylographiées
Hamburg	1986	83		26

Requesting Department / Ministère-Client: DFO

Translation Bureau No. / Notre dossier nº: 3287208

Branch or Division / Direction ou Division: IPB

Translator (Initials) / Traducteur (Initiales): IJ

Person requesting / Demandé par: N. Johnson

SEP 14 1987

Your Number / Votre dossier nº:

Date of Request / Date de la demande: 87/07/?6

5228

Canada

TRANSLATION NOT EDITED FOR PUBLICATION
TRADUCTION NON DESTINÉE À LA PUBLICATION

SEC 5-111 (84-10)

Secretary of State | Secrétariat d'État

MULTILINGUAL SERVICES DIVISION – DIVISION DES SERVICES MULTILINGUES

TRANSLATION BUREAU | BUREAU DES TRADUCTIONS

Client's No.–N° du client	Department – Ministère	Division/Branch – Division/Direction	City – Ville
	DFO	IPB	Ottawa
Bureau No.–N° du bureau	**Language – Langue**	**Translator (Initials) – Traducteur (Initiales)**	
3287208	German	IJ	SEP 14 1987

Contributions to the Systematics of the African Naididae (Oligochaeta) III. Studies on the Qualitative and Quantitative Chaetotaxonomy of the Naididae

By

REINMAR GRIMM

(With 9 Figures and 2 Tables)

Abstract

Using an SEM to study the details of setal structure in African Naididae the author found that features which have been up to now considered to be principally different turned out to be only gradually different, e. g. most of the bifid needle setae turn out to be pectinate or the hair setae turn out to be more or less roughly serrated (= "chipped").

Measuring the setal lengths in almost all of the investigated naidid specimens led to the result that at least the measurements of the needle and ventral setae obtain the quality of taxonomically utilizable characteristics.

5328

SEC 5-25 (Rev. 82/11)

Canada

1. Introduction (p. 102)

The Naididae are still considered to be Oligochaeta that are easy to determine. They are transparent, at least while alive, which "permits a delightful view of the internal organs at work" (KAESTNER 1954/55); their well differentiated setae are features that are easy to describe and which "chaetotaxonomy" uses in order to characterize the genera and species. Up to now chaetotaxonomy has regarded the setal features as largely constant. In the past, investigators have therefore often based descriptions of species on only a few specimens or even only one type specimen, so that it was not possible to investigate the range of variations in taxonomically relevant features. While working with numerous African Naididae, I encountered a problem: the greater the number of animals used in the investigation, the less it was possible to distinguish between certain species. I realized that the setal form is far more variable than hitherto assumed, for example by SPERBER (1948), while on the other hand the absolute lengths of the setae can be relatively constant. Here a chaetotaxonomic problem concerning the Naididae becomes apparent: the often minute differences between setae are frequently given too much weight as systematic characteristics, especially (p. 102)
as their variability is still largely being disregarded. Therefore it is understandable that species of Naididae are occasionally described on the basis of setal features that later turn out to be environmentally induced modifications of features of already known species (cf. the studies by LODEN & HARMAN 1980 on Pristina aequiseta). To put it differently: As far as the setae of the Naididae are concerned, morphological differences which were hitherto considered to be fundamental and thus became taxonomic features, may turn out to be gradual differences, if sufficiently precise investigative methods are employed. This holds true for the formation of intermediate teeth

in the case of pronged needle setae as well as for the "chipped" appearance of the hair setae (see p. 14). In SEM investigations the pronged needle setae of the African Dero species and of the Aulophorus species of the furcatus group turned out in fact to be pectinate setae (sometimes recognizable even under the light microscope), see Figs. 16-18. This has often led to errors in identifying species, especially of the genus Aulophorus. The size of the needle setae determines whether the intermediate teeth (which are almost always present) can be recognized; therefore using the size of the setae as distinguishing features in the first place is the only method that makes sense. Not only in the genera Dero and Aulophorus, but also in Nais and Pristina were pectinate setae found to occur in species for which pronged needle setae had been assumed to be characteristic. The formation of intermediate teeth together with pronged needle setae and the "chipping" of hair setae are much more frequent phenomena among Naididae than had been hitherto assumed.

If in the case of Naididae we look for taxonomically usable structures other than setae, we discover that this group has comparatively few distinguishing features. Since in the case of the Naididae asexual reproduction takes place over long periods of time, sexual organs which can usually be considered the most reliable species-specific structures in Oligochaeta, are formed only temporarily and only under certain conditions. Therefore, as far as the Naididae are concerned, setae remain the most important embodiments of taxonomic features. However, on the basis of what is known about the African Naididae investigated, two requirements must be met: One, the differences between the features of the setae to be compared have to be really significant; two, the size of the setae as well as its shape has be included in the evaluation.

My intensive studies of African Naididae in particular arose from the opportunity to gather a large collection of these animals during a series of expeditions to various regions of Africa. As a result of my preoccupation with the problems of chaetotaxonomy, my work on the African Naididae led to systematic study focussing on this particular aspect. It centres around a critique of the taxonomy of the Naididae up to now, i.e. in particular an analysis of the fundamental study by SPERBER (1948): "A taxonomical study of the Naididae", the works of BRINKHURST (1966 and 1970) and the large, comprehensive work by BRINKHURST & JAMIESON (1971): "Aquatic Oligochaetae of the world", all of which build on the above-mentioned study by SPERBER.

Especially in the case of applied ecological investigations (such as the ones undertaken in recent years in South Africa in connection with a major program to list all bodies of water) attempts should always be made to take the species as the smallest taxonomic unit. As far as the Oligochaeta, especially the Naididae, are concerned which are of such importance for the biological economy of bodies of water, this should be possible given our modern knowledge.

(p. 103)

The system in use at the moment for the Naididae is in many areas in urgent need ot revision. This has been shown clearly during the study of the African forms. Some work is still required to develop perhaps some additional and better systematic criteria than those in use today. One aspect in particular is serious, namely that systematically relevant structures in Naididae are often described in the literature only on the basis of live or freshly killed animals, because it is only in these that the structures can be recognized at all or at least can be recognized better than in preserved

animals. In most cases there are no indications as to what changes have been brought about by fixing or preserving of specimens. However, in future more recognition will have to be given to the fact that in most investigations involving Naididae, the specimens exist as preserved animals which have to be identified as such, and that the setal features are decisive.

2. Material and Method

The African Naididae investigated by me come from various collections or were collected by myself during several field trips to Africa. I would like to take this opportunity to offer my warmest thanks to all the institutions and persons who were kind enough to let me have Naidid material for me to work with. The following material was available to me:

The collection of Albany Museum, Grahamstown, S. Africa, consisting of animals from various find locations in S. Africa, which had been preserved in alcohol. In addition, some microscopic preparations were investigated for the purpose of comparison.

The collection of the Transsahara-Central Africa Expedition 1969 (cf. GRIMM 1974); these specimens were collected by me.

A collection from bodies of water in southern Sudan (expedition to southern Sudan 1975); these specimens were collected by me.

A collection from bodies of water in S. Africa (expedition 1976); these specimens were collected by me.

A collection from two bodies of water in Ethiopia (expedition of H. OBOUSSIER and D. ERNST 1976).

The collection of Dr. F.C. VILJOEN from the Elsburgspruit, S. Africa. Preserved animals.

The collection of Dr. R.F. BRINKHURST from various locations in S. Africa. Microscopic preparations (for the purpose of comparison).

The collection of the British Museum (Natural History), London, from various locations. Microscopic preparations (for the purpose of comparison).

In order to study the animals in detail, they were made into full microscopic preparations. Those that were strongly pigmented were not stained, the others were completely stained with borax carmine and, using clove oil, were embedded into the phase contrast embedding medium L 15 of the firm Zeiss. (p. 104) Several stains and various embedding media were tested. Eventually those mentioned proved to be the most practical ones: when they were used most of the animals' soft parts remained recognizable; those parts frequently have to be resorted to as additional differential diagnostic features. I regard it as undesirable to embed Naididae (after first compressing them) into the kind of embedding medium which allows only the setae to be recognized (these are often swollen and deformed as a result). The animals I prepared were therefore as little compressed as possible. The advantage of this method of embedding is that at least the intestinal tract with all its details usually remains clearly recognizable. In my opinion this fact largely outweighs any disadvantages (the animals are occasionally not accessible to oil immersion lenses, and the setae are often not in the image plane). Altogether, some 1300 specimens of Naididae were treated in this way.

The animals which had been made into permanent microscopic preparations were studied using phase contrast (setae) or interference contrast

(soft parts). The fine structure of the setae was studied in more detail with the aid of a scanning electron microscope. For this purpose animals preserved in Formal were either air-dried or dried according to the critical point method.

The systematic investigation of the African Naididae has shown that the absolute length of the setae is of taxonomic significance. The setae were measured according to the instructions given by SPERBER (1948; cf. Fig. 1). SPERBER points out the great difficulties that are, in her opinion, inherent in the statistical recording of the setal lengths: "The variation in length with the position of the setae, however, makes the value of such statistics fairly small. To give it any significance one ought to measure certain setae in certain bundles, e.g. the outermost and innermost seta in the left bundle of some specified segments from a large collection of material, and calculate the mean, and the standard error, etc. for each seta..." SPERBER alleges that this method is too wasteful of time and material to be of any really practical value. Above all, she suggests that there is scarcely any method or preparation which guarantees that if a large number of animals is investigated, the seta to be measured is always the same seta in the same segment.

I have measured hair setae, needle setae and ventral setae of practically all the African Naididae investigated by me and discovered that the intra-individual variability of the setae roughly corresponds to the inter-individual variability. As a result, the following method for establishing setal measurements was used: In the case of each investigated animal one randomly chosen seta of each setal type from one of the segments in front of the budding zone was measured, and the result was entered into a list as the measurement for the setal type and the animal in question (the choice of the

setae to be mesured was random, because only a few setae lie in a plane suitable for measuring at any one time; in the majority of cases it is impossible to decide whether the seta that has been measured is the shortest, the longest or an intermediate seta in the setal bundle in question). In this way a random sample (as many individuals of a population as possible) was obtained and its mean value m and the standard deviation s were computed. In the tables listing the setal measurements the mean value of setal lengths is given as m (length in µm) = m ± s. In order to compare two or more mean values the t test and the one-way analysis of variance (according to the methods described by KREYSZIG 1965 and CAVALLI-SFORZA 1974) were used. In each case α = 5% was chosen as the level of significance

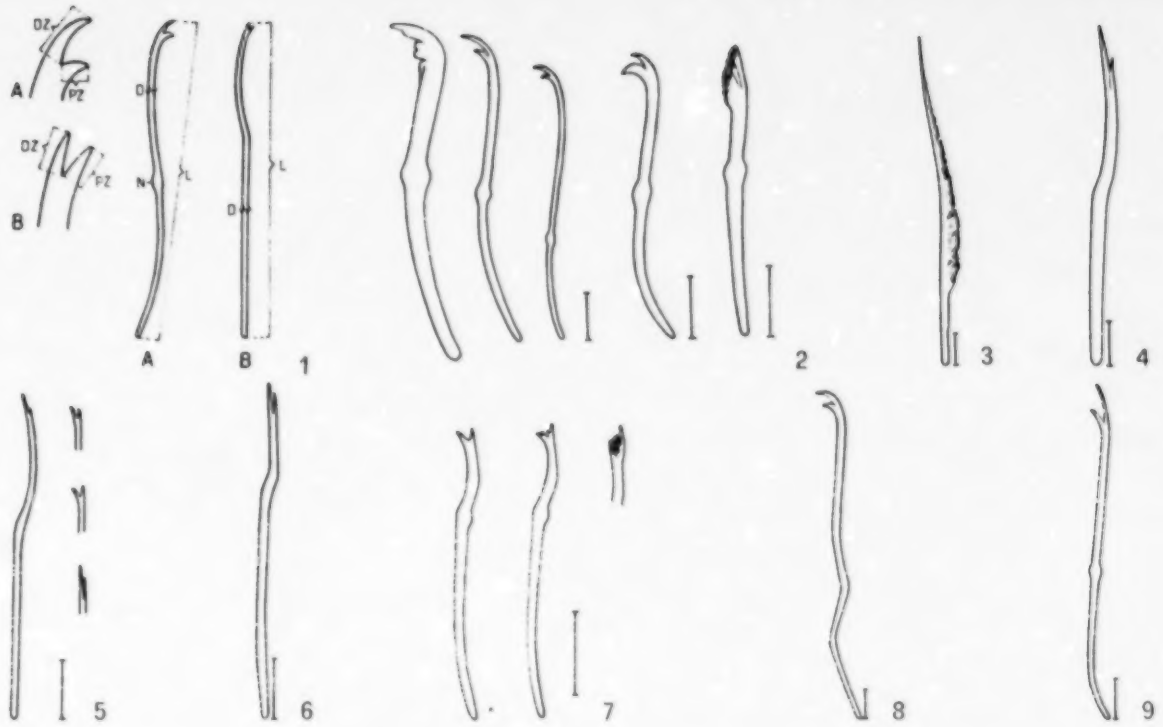

Fig. 1-9. -1: Setal dimensions measured on: A ventral seta, B needle seta, D=thickness DZ=distal tooth, L=length, N=nodulus, PZ=proximal tooth. -2: Rhopalonais africana. From left to right: giant seta in II, other ventral seta in II, ventral seta in III-V, posterior ventral seta. Needle seta. -3: Dero pectinata. Hair seta. -4: Allonais paraguayensis. Needle seta. -5: Pristina menoni. Needle setae (various types). -6: Pristina jenkinae. Needle seta. -7: Pristina osborni. Needle setae. -8: Stylaria fossularis. Posterior ventral seta. -9: Stephensoniana trivandrana. Ventral seta. -Scale 10 µm.

3. The Naidid Setae as Carriers of Taxonomic Features

(p. 106)

As a rule, in the Oligochaeta, each segment with the exception of the metastomium and some posterior body segments, has on each side two setal sacs, one on top of the other, the setae of which can be homologized with those of the dorsal or ventral branch of the parapodium of the Polychaeta. The setae are of ectodermal origin and consist of chitin as well as a protein component (AVEL 1959). The highest degree of setal differentiation among the Oligochaeta is reached in the Naididae. As a rule three kinds of setae are formed: hair setae and needle setae in the dorsal setal sacs and ventral setae in the ventral sacs. A full complement of setae on the segment of a Naidid consists of two dorsal setal sacs, each with one or more hair setae, or one or more needle setae, as well as two ventral setal sacs each with a bundle of ventral setae. The first body segment (mouth segment = metastomium) of the Naididae always lacks setae. The other body segments are equipped with setae in different ways according to the various genera. In the genus Chaetogaster dorsal setae are missing altogether, while ventral setae are missing in segments III-V. Some genera do not form hair setae (see below). Other genera or species lack the dorsal setae in a number of anterior body segments (the number being constant throughout the genus or species in question). In most cases the ventral setae of these segments display a shape that deviates from that of the other ventral setae. Among the African species of Naididae Rhopalonais africana (see Fig. 2) attains the highest degree of differentiation of this kind in its ventral setae. The older literature occasionally mentions "cephalisation" in connection with this phenomenon (for example in MICHAELSEN 1914). However, there is no genuine cephalisation in the Naididae in the same way as in the Polychaeta. However, taxa with differentiated setation of the anterior end, as described, must be regarded as

more derived than those in which the dorsal setae start much further towards the anterior end and the anterior and posterior ventral setae do not differ.

Setae belong to the taxonomically most important structures in the Naididae, which are otherwise relatively lacking in features. The classic "chaetotaxonomy" of the Naididae is essentially based on qualitative features, i.e. those relating to form, of the setae; however, it reaches the limits of its usefulness where, without taking into account the variability, minute differences in setal form which are hardly recognizable are regarded as taxonomically relevant. For example, according to identification keys employed at present for the genus Pristina, needle setae and ventral setae are used to identify the five species of the Pristina rosea group (P. amphibiotica, P. jenkinae, P. menoni, P. rosea and P. idrensis). However, during my investigation of the African material I came to the conclusion that separating the above-mentioned five species of Pristina using the criteria employed so far is extremely questionable: the needle setae occur in all imaginable combinations and variations, sometimes in the same animal, in such a way that one would have to assign the anterior end to one species and the posterior end to another. The ventral setae are small in all the species and bear small teeth (on average approx. 2 µm), therefore differences in the length of the teeth are in the order of magnitude of $\lesssim 1$ µm. Under these circumstances the following alternatives can hardly be used for differentiating between two species: "Anterior ventral setae with upper tooth slightly longer than lower, the difference less posteriorly (P. rosea) - Anterior ventral setae with upper tooth as long or longer than lower, shorter posteriorly (P. amphibiotica)" (BRINKHURST & JAMIESON 1971)

An essential outcome of my investigation of the African Naididae is the proof that setal length as well as the number and form of the setae are characteristic features . (p. 107)

Up to now quantitative features have hardly been considered important in the systematics of the Naididae. In the literature it has been common to quote the range of variation of setal lengths and to give certain individual measurements of other organs (e.g. proboscis, genital organs, gills), but mostly without pointing out the condition of the specimen (freshly killed or preserved). In the course of investigating the African Naididae, an initial step was taken towards statistically evaluating the range of variation of the absolute setal lengths (and also the number of segments) by determining the mean value and the range of scatter. The setae of the Naididae (especially needle setae and ventral setae) turned out to have a much more constant length than one would have assumed according to the range of variation of this value. The standard deviation of the mean setal lengths in needle setae and ventral setae amounts on average to less than 10% of the mean setal length; in hair setae the standard deviation is 15.1% (see Table 1). Thus at least the measurements of the needle setae and ventral setae of the Naididae assume the quality of taxonomic features. It is remarkable that the lengths of the needle setae and ventral setae (specifically those of approximately the middle section of the body) largely correspond. Table 1 enables us to calculate a ratio of 1.1 ± 0.2 for ventral setae to needle setae, that is to say, the (posterior) ventral setae are on average 0.9 to 1.3 times as long as the needle setae of the same region of the body.

SPECIES/VARIETY	VBv			VBh			NB			HB		
	m	s	s%	m	s	s%	m	s	s%	m	s	s%
Chaetogaster limnaei	87	8,6	9,9	53	4,6	8,7						
Ch. diaphanus	147	11,6	7,9	110	7,2	6,5						
Ch. diastrophus	91	8,5	9,3	69	6,0	8,7						
Homochaeta proboscidea				40	4,7	11,5	38	2,7	7,1			
Nais communis				76	6,7	8,8	58	6,5	11,2	185	17,4	9,4
N. variabilis f. typica	84	7,5	8,9	74	5,5	7,4	60	3,1	5,2	274	71,6	26,1
N. variabilis ssp. simplex (1)				70	3,7	5,3	58	4,9	8,4			
- " - (2)	88	7,1	8,1	73	4,7	6,4	56	6,0	10,7	161	19,7	12,2
- " - (3)				77	6,9	9,0	64	4,5	7,0			
N. elinguis (3)				87	4,5	5,2	76	2,5	3,3			
- " - (4)				97	7,3	7,5	99	8,2	8,3			
Slavina appendiculata	125	4,6	3,7	107	9,8	9,2						
Stephensoniana trivandrana	73	7,8	10,7	81	9,0	11,1	38	2,4	8,9	175	26,7	15,3
Allonais paraguayensis				103	7,7	7,5	107	15,7	14,7	271	70,2	25,9
A. pectinata				80	3,7	4,1	44	4,1	9,4	240	18,0	7,5
A. ranauana				57	4,8	8,4	60	7,0	11,7	168	17,3	9,2
Dero digitata	141	18,0	12,8	110	6,9	6,3	95	9,3	9,8	290	36,9	12,7
D. cooperi	109	10,9	10,0	79	4,4	5,6	84	6,5	8,6	183	16,8	9,2
D. nivea	95	8,8	9,3	63	4,9	7,8	54	4,7	8,7	139	25,7	18,5
D. oblongata	110	7,1	6,5	80	4,5	5,6	75	4,3	5,7	198	14,3	7,2
D. reviensis	75	4,8	6,4	45	2,9	6,4	40	3,2	8,0	95	10,6	11,2
Rhopalonais africana	81	6,7	8,3	48	3,0	6,5	42	3,2	7,6	85	7,8	9,2
Aulophorus furcatus	68	6,3	9,3	60	5,9	9,8	51	6,4	12,5	140	28,2	20,1
A. africanus	89	5,4	6,1	82	5,0	6,1	79	6,2	8,3	303	51,6	17,0
A. tonkinensis	89	6,1	6,9	50	3,7	7,4	57	2,9	5,1	108	7,0	6,5
A. ghanensis	124	12,7	10,2	72	4,8	6,7	87	8,2	9,4	162	14,0	8,6
A. flabelliger	96	9,6	10,0	46	2,8	6,1	54	5,1	9,4	93	8,2	8,8
Pristina osborni				38	3,0	7,9	34	3,0	8,8	98	15,0	15,3
P. amphibiotica				48	3,0	6,3	50	6,0	12,0	123	22,0	17,9
P. jenkinae				51	2,0	3,9	57	7,0	12,3	207	59,0	28,5
P. menoni				49	4,0	8,2	52	5,0	9,6	173	33,0	19,1
P. aequiseta	54	4,0	7,4	45	3,0	6,7	39	4,0	10,3	144	24,0	16,7
P. longiseta	95	4,0	4,2	59	7,0	12,9	48	6,0	12,5	226	55,0	24,1
P. synclites	78	4,0	5,1	69	4,0	5,8	78	7,0	10,0	330	67,0	20,3
n (s%)			8,2			7,4			9,1			15,1

Table 1: Mean values and standard deviations of setal lengths of the African Naididae. -Abbreviations: VBv = anterior ventral setae, VBh = posterior ventral setae, NB = needle setae, HB = hair setae, m = mean setal length in µm, s = standard deviation of the mean value, s% = standard deviation expressed in per cent of the mean value. -The numbers in brackets mean: (1) Central Africa, (2) Southern Sudan, (3) South Africa, (4) Tenerife

Stating the setal length at the same time says something about the size of the investigated animals. Larger Naidid species have relatively longer setae. If the size of the animals in a species of Naididae is to be characterized (in terms of setal length), it is sufficient to state the mean lengths of the posterior ventral setae (which are also usually the ones easiest to measure). The method of measuring setae, which is represented in this paper, is the easiest possible and very suitable for practical purposes, since only one ventral seta per animal has to be measured.

In the following the morphological peculiarities of the three setal forms are described.

Hair setae

Hair setae occur in all genera of Naididae except Chaetogaster, Amphichaeta, Paranais, Homochaeta, Uncinais and Ophidonais. They are usually thin and sufficiently elastic not to break off, except in rare instances, even in preserved animals. SPERBER (1948) states that they "are usually smooth... However, in most of the species of the genera Pristina, Stylaria, Ripistes and Vejdovskyella the hair setae are equipped with one or two rows of saw teeth..." In the literature such hair setae are characterized as "serrated".

The investigation of the African Naididae revealed a phenomenon that is widespread in this family: The hair setae appear to have been cut into repeatedly as if with a knife, with the result that pieces stand up from the surface (Table I, Fig. 1-3). I call this phenomenon "chipping" and the state of the hair setae "chipped". The hair setae may be chipped finely or coarsely; the chipping may be dense or sparse; the chips may be long or short, and they may be arranged in one or more rows. In most cases only one side of the hair seta is affected. In an aqueous medium the phenomenon can only be seen

very vaguely (in this case the hair setae are called "serrated"). With the aid of the phase contrast embedding medium used by me, chipping of hair setae can be seen in, among other, Nais elinguis, Dero digitata, Aulophorus africanus, Stephensoniana trivandrana and Pristina menoni. Under the electron microscope the hair setae appear as bundles of parallel fibres (see Table I, Fig. 4). The "shavings" curled back from the chipped hair setae can be interpreted as the end pieces of fibres which are shorter than the hair setae. It is possible that the phenomenon of chipping is a sign of the animal having reached a certain age and a sign of wear and tear where the ends of the individual fibres detach themselves from the rest of the structure. In animals dried according to the CP method extremely fine chipping can be detected under the electron microscope. The existence or absence of "serrated" hair setae therefore turns out to be an unsuitable taxonomic feature, because the visibility of chipped hair setae is first and foremost a question of optics and of the embedding medium, and because "serration" is only one extreme case within a great variety of chipping phenomena.

Apart from smooth hair setae and hair setae chipped in various ways there is a third type, the frankly pectinate hair setae, which occur, for example, in Dero pectinata (see Fig. 3).

The length of hair setae fluctuates more than that of any other setal type, both within one individual animal and among the members of one population. In order to arrive at comparable measurements the longest hair seta of an animal was measured whenever possible. Therefore the length data in Table 1 constitute extreme values as far as hair setae are concerned. These values, too, fluctuate considerably: the fluctuation ranges from 6.5% of the mean length of hair setae in the case of Aulophorus tonkinensis to 28.5% in the case of Pristina jenkinae, with the average being approximately 15.1%.

(p. 109)

This means that the absolute length of the hair setae can only provide an indication as to the size of the animal but cannot be used as a taxonomic feature.

Needle Setae

Needle setae occur in all genera of Naididae except Chaetogaster which does not have any dorsal setae at all. Needle setae exhibit the greatest variety of form and belong to the most important taxonomic features in the family. Needle setae may have a pronounced nodulus, as do the ventral setae; there may also be just a suggestion of a nodulus, or a nodulus may be lacking altogether. Many needle setae come in the shape of a bayonet: the proximal, longer part is more or less straight and elongated, the distal, shorter one is bent like a bayonet (of slightly sickle-shaped). The position of the nodulus is marked by the transition from the proximal to the distal part (see Fig. 1).

Apart from single-pointed needle setae similar to hair setae of the kind which occur in Stylaria and Stephensoniana, I distinguish between three types of multi-pointed needle setae which I consider to be fundamentally different; namely the split type, the pronged type and the palmate type.

1. The Split Type

The type of needle seta is double-pointed, and the proximal tooth (i.e. the one originating on the concave side of the setal end) is the strongly dominating one. The distal tooth (the one originating on the convex side of the setal end) is very thin and underdeveloped by comparison and tends to diminish in size with the result that the setae may become single-pointed. I call these needle setae split because photographs taken with the aid of an electron microscope reveal that the distal tooth is split off in exactly the same way as the "chips" in the case of hair setae.

Split setae occur in the case of Allonais paraguayensis (see Fig. 4 and Table I) and in Pristina menoni (see Fig. 5 and Table I, Fig. 6). The needle setae of Pristina jenkinae (see Fig. 6), which unfortunately could not be investigated under the electron microscope up to now, probably also belong to this type. The fine structure of the needle setae of the split type points to their derivation from hair setae. Thus they represent an original type of needle setae, as do the pronged needle setae, which resemble ventral setae.

2. The Pronged Type

The needle setae of this type end in at least two well developed teeth. Their form may be close to that of the ventral setae (see those) in the same way as, for example, the needle setae of Pristina osborni are (see Fig. 7); on the other hand, they may also be equipped with extremely short, parallel and such densely arranged teeth that they give the impression of being bluntly single-pointed (e.g. Nais variabilis ssp. simplex, see Table I, Fig. 7). A widespread phenomenon among pronged needle setae is the formation of intermediate teeth between proximal and distal teeth, i.e. of pectinate needle setae (pectinate setae, see Table I, Fig. 8 and 9, Table II, Fig. 1 and 2). The intermediate teeth may be so fine that they are below the limit of resolution, unless the optics are first class and the embedding media are favourable. In any event, they are sure to be visible under an electron microscope. Thus the situation is the same in the case of pectinate setae and serrate hair setae: in general, the formation of intermediate teeth should be possible in the case of all pronged needle setae. (p. 110)

Pectinate setae have hitherto been recognized and considered to be a reliable taxonomic feature, as long as they were large enough or sufficiently

coarsely serrated. As optical instruments improved there were more and more wrong identifications, because pectinate setae occurred in species which should only have had pronged needle setae. Such mistakes could only have come about because up to then it was exclusively the shape of the setae but never their size which was taken into account. I found pectinate setae in all species of Dero and Aulophorus that have pronged needle setae, as well as in Pristina osborni and Nais elinguis. As early as 1980 LODEN & HARMAN reported having found three-pointed and pectinate needle setae in Dero, Pristina and Nais, and they regard these deviations as "ecomorphic variations". In the collection of Louisiana State University they found specimens of Pristina osborni and Nais communis in which the needle setae of the anterior zooid were double-pointed and those of the posterior zooid were three-pointed or pectinate. "This is apparently a condition triggered by differing environmental conditions whereby the generation of the older, anterior setae was influenced by one set of environmental conditions that had become altered when the younger, posterior segments were formed". What kind of environmental conditions are the decisive factor here, or to what extent we are dealing with a hitherto unrecorded modificability of the needle setae independent of external influences needs to be investigated in more detail.

3. The Palmate Type

Probably originating from pectinate setae, the palmate setae constitute the most derived form of needle setae. Their shape is extremely constant. They occur only in those genera that do not exhibit split setae, in genera whose pronged setae have a tendency to form intermediate teeth and in genera that have to be considered as derived on the basis of other features as well, for example Dero , Rhopalonais (see Fig. 2 and Table II, Fig. 3) and Aulophorus (see Table II, Fig. 4-6).

In those animals that were investigated in this regard, the length of the needle setae fluctuates on average by 10% (9.1 ± 2.5) of the mean setal length (see Table 1). The smallest fluctuation was found in the case of Nais elinguis from South Africa (3.3%), the largest in Allonais paraguayensis (14.7%). The difference in size is very obvious in the case of needle setae that are congruent in shape and found in the species Aulophorus ghanensis and A. tonkinensis or in the series of species A. pectinatus, A. africanus, A. furcatus. BRINKHURST (1966) would without any doubt have been able to ascertain that the specimens of Aulophorus he was investigating could not possibly belong to the species A. pectinatus, if he had taken into account the setal length in his taxonomic investigations.

Ventral setae

As a rule ventral setae are of the typical pronged variety (rarely is a tooth missing) with a distinctly formed nodulus. They usually occur in all segments starting with II (they are absent in segments III-V only in the case of Chaetogaster). The ventral setae are not all the same: there are differences among the setae of one setal bundle, as well as between the ventral setae of one or more anterior segments and those of the segments located closer to the posterior end in many genera and species. Towards the posterior end of the animals the number of ventral setae per bundle usually decreases, and the setae become at the same time shorter and thinner. (p. 111)

Frequently there is a clear difference between the ventral setae of those segments at the anterior end of the body which are freshly formed in the budding zone after transverse fission, and the ventral setae of the remaining segments: the former are usually longer, straighter and more elongated and thinner than the latter; their teeth are longer, and their noduli

are usually situated proximal to the middle of the setae. Such a clear distinction between anterior and posterior ventral setae occurs in most species of the genus Nais, in Dero, Rhopalonais, Aulophorus and some species of Pristina. In Allonais a difference exists between anterior and posterior ventral setae but it is not particularly distinct.

Some genera exhibit enlarged, sometimes coarse ventral setae which are then called giant setae. In Rhopalonais africana segment II (the first segment with setae) is equipped with such giant setae; in Pristina aequiseta setae in segments IV or V or in both may be formed as giant setae. In Pristina longiseta the ventral setae of segment III tend to be enlarged. Nais pardalis, N. bretscheri and Vejdovskyella intermedia are to date the only Naididae found exclusively outside Africa that have giant setae.

The ventral setae occurring in the genera Chaetogaster, Stylaria and Stephensoniana exhibit a particular shape. In Chaetogaster the ventral setae have a more or less sharp kink between proximal end and nodulus; in Ch. limnaei the prongs are unusually strongly bent. The ventral setae of Stylaria exhibit a characteristic double kink and lack a nodulus (see Fig. 8), and in Stephensoniana finally the prongs of the ventral setae are hardly bent at all (see Fig. 9).

If we disregard the special shapes discussed here we can say that in the majority of the Naididae the ventral setae present a rather uniform appearance: they are more or less S-shaped and possess a distinct nodulus positioned more or less proximal to the middle of the setae in the anterior segments, or more or less medianly in the middle segments, and more or less distal to the middle of the setae in the posterior segments. The setal teeth

are moderately bent; the proximal tooth is thicker than the distal one; the distal tooth tends to be longer than the proximal one in the setae of the anterior segments; further towards the posterior end the teeth are usually of equal length, or the proximal tooth might even be longer than the distal one. Because of its uniformity the shape of the ventral setae can hardly be utilized for purposes of taxonomy, with the exception of the few cases mentioned above and a few additional ones. However, the length of precisely those ventral setae which differ least of all regarding their shape is all the more reliable as a feature: in the middle section of the body just in front of the budding zone. The "posterior ventral setae" in question here exhibit the least average diviation from the mean setal length (cf. Table 1) at 7.4 ± 2%. The largest deviation at 12.5% is found in Pristina longiseta, the smallest at 3.9% in P. jenkinae.

4. Conclusions and Recommendations

To start with, the fact that the standard deviation of the mean lengths of needle setae and ventral setae is less than 10% of the mean setal lengths has been proved only as far as the African Naididae investigated by me are concerned. This has yet to be verified in the case of all the other species. Further studies will also be needed to reveal whether the setal measurements found in African Naididae are valid all over the world or only in Africa. As Table 1 shows, in Africa setal lengths are surprisingly uniform even in populations that are widely dispersed (Southern Sudan, Central Africa, South Africa), and they can easily be used for identifying species of Naididae. (p. 114)

In order to be able to verify whether the results of the "quantitative chaetotaxonomy" treated in this paper are generally valid, and in order

to determine the size of the Naididae more exactly with the aid of setal measurements in future, the following data concerning setation should be provided uniformly:

1. Number of animals investigated (particularly number of setae measured);
2. Number of setae per bundle of hair setae, needle setae, anterior and posterior ventral setae;
3. Maximum and minimum values of setal lengths in µm (range of variation)
4. Average length of setae in µm, stating standard deviation.

See Table 2 for a representation of these values in tabular form. Data for the posterior ventral setae are sufficient for a "short characterization".

Table 2: Dero digitata. Numbers of setae and setal measurements (16 specimens were measured)

	① VB II-V	② VB w.h.	③ NB	④ HB
⑤ Angaben in lit.				
⑥ Anzahl p. B.	3 – 6	2–5	1	1
⑦ Länge in µm	135 – 165	86 – 123	85 – 121	294 – 390
⑧ Eigene Messungen				
⑨ Länge in µm	117 – 167	97 – 125	82 – 116	260 – 338
⑩ m (Länge in µm)	141 ± 18,0	110 ± 6,9	95 ± 9,3	290 ± 36,9

Translation key:

1. Ventral setae in segments II-V
2. Ventral setae further towards the posterior end
3. Needle setae
4. Hair setae
5. Data in the literature
6. Number per bundle
7. Length in µm
8. Own meanurements
9. Length in µm
10. m (length in µm)

5. Conclusion

In the family Naididae setae are the most important carriers of systematic features. The "chaetotaxonomy" of the Naididae is based on this fact. In order to study the fine structure of the setae a scanning electron microscope was used to investigate African Naididae. Result: structural differences which were considered fundamental up to now (i.e. pronged as against pectinate needle setae, smooth as against serrated, i.e. "chipped", hair setae) turned out to be only differences of degree. With sufficient magnification most of the pronged needle setae turned out to be pectinate setae, and most hair setae proved to be more or less finely chipped (for example in the genera Dero and Aulophorus).

In most of the investigated African Naididae the lengths of the various setae were found with the aid of a simple, easily reproducible procedure. In the course of this it became apparent that the mean absolute length of the setae can also be used to characterize species of Naididae. The standard deviation of the mean setal lengths in needle setae and ventral setae amounts to less, on average, than 10% of the mean setal lengths; in the case of the hair setae the deviation amounts to 15.1%. This is true in Africa for populations that are widely dispersed. In this way at least the measurements of needle setae and ventral setae in the Naididae assume the quality of taxonomically usable features.

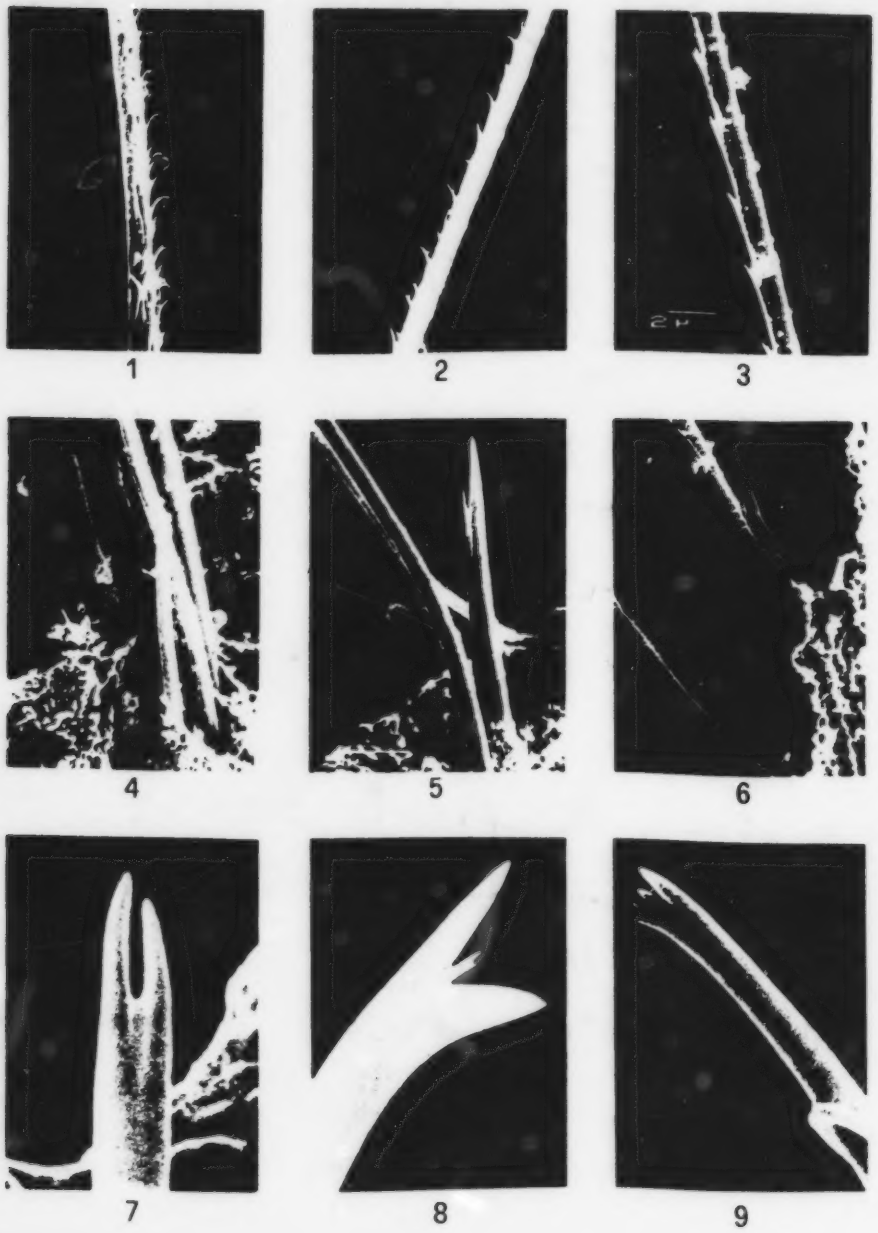

Table I

Fig. 1-3: Hair setae. 1 = Pristina menoni (3300 x), 2 = Aulophorus africanus (1600 x), 3 = Pristina longiseta, Fig. 4: Pristina longiseta, dorsal bundle of setae (5500 x), Fig. 5: Allonais paraguayensis, needle seta (2200 x), Fig. 6: Pristina menoni, two dorsal bundles of setae, 7 = Nais variabilis ssp. simplex (15 800 x), 8 = Dero digitata (3400 x), 9 = Dero raviensis (4500 x)

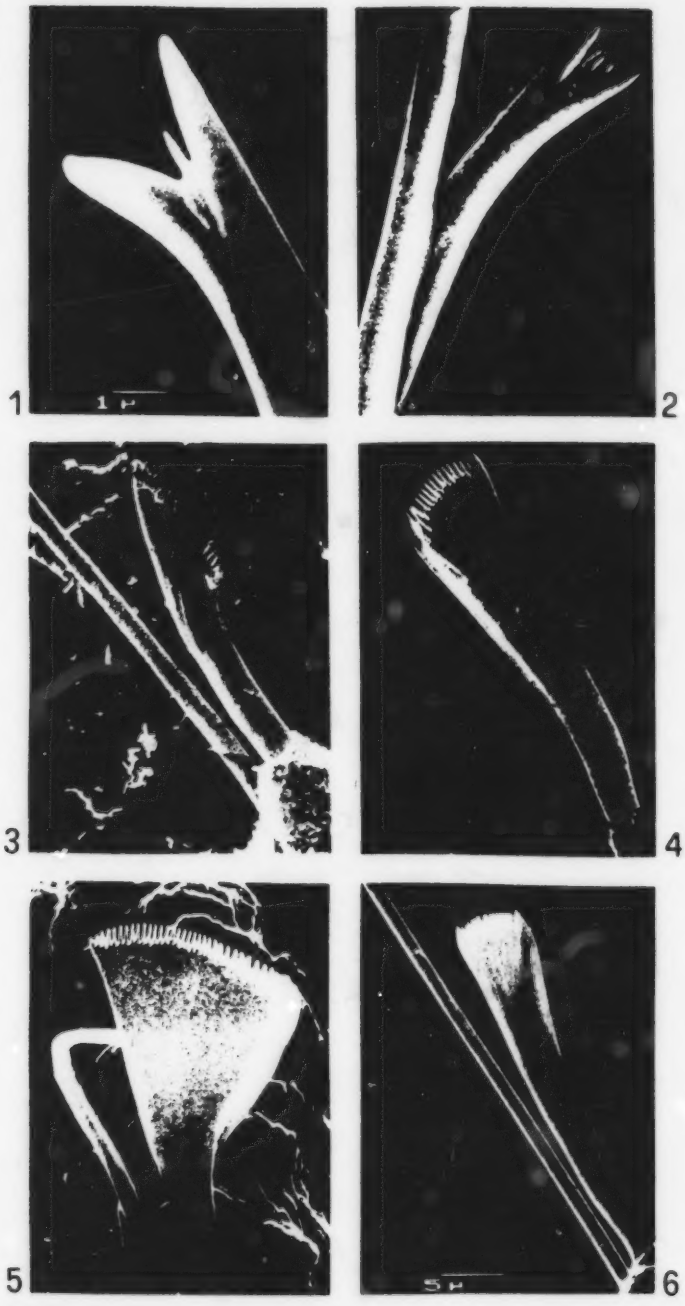

Table II

Fig. 1-6: Needle setae, 1 = Aulophorus africanus, 2 = Aulophorus furcatus (4000 x), 3 = Rhopalonais africana (1700 x), 4 = Aulophorus tonkinensis (1700 x), 5 = Aulophorus flabelliger (2700 x), 6 = Aulophorus ghanensis.

6. Bibliography

AVEL, M., 1959: Classe des Annélides Oligochètes. In: GRASSE, P. P.: Traité de Zoologie, 5 (1): 224 pp. Paris.

BRINKHURST, R. O., 1966: A contribution towards a revision of the aquatic Oligochaeta of Africa. – Zoologica Africana, 2: 131–166. Kapstadt.

– & JAMIESON, B. G. M., 1971: Aquatic Oligochaeta of the world. – 860 pp. Edingburgh (Oliver & Boyd).

① CAVALLI-SFORZA, L., 1974: Biometrie. Grundzüge biologisch-medizinischer Statistik. – 212 pp. Stuttgart (Gustav Fischer).

② GRIMM, R., 1974: Einige Oligochaeten aus Nigeria, dem Tschad und der Zentralafrikanischen Republik. – Mitt. Hamburg. Zool. Mus. Inst., 71: 95–114. Hamburg.

③ KAESTNER, A., 1954/55: Lehrbuch der Speziellen Zoologie. Teil I: Wirbellose, 1. Halbband, S. 554. Berlin (Gustav Fischer-Verlag).

④ KREYSZIG, E., 1965: Statistische Methoden und ihre Anwendungen. – 422 pp. Göttingen (Vandenbock & Ruprecht).

LODEN, M. S. & HARMAN, W. J., 1980: Ecophenotypic variation in setae of Naididae (Oligochaeta). – In: BRINKHURST, R. O. & COOK, D. G.: Aquatic Oligochaete biology. 529 pp. New York and London (Plenum Press).

⑤ MICHAELSEN, W., 1914: Beiträge zur Kenntnis der Land- und Süßwasserfauna Deutsch-Südwestafrikas. Oligochaeta. – Reg. Hamb. Deutsch Südwest-Afrikas. Studienreise, 9: 137–182, Hamburg.

SPERBER, C., 1948: A taxonomical study of the Naididae. – Zool. Bidr. Upps., 28: 1–318. Uppsala.

1. Biometry. The Rudiments of Biological-Medical Statistics
2. Some Oligochaeta from Nigeria, Chad and the Central African Republic
3. Textbook of Special Zoology. Part I. Invertebrates. First half of volume
4. Statistical Methods and their Applications
5. Contributions to the Knowledge of the Terrestrial and Freshwater Fauna in German Southwest Africa. Oligochaeta